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CHAPTER SEVEN

Climate-Driven Range Shifts Within Benthic Habitats Across a Marine Biogeographic Transition Zone

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Abstract

Anthropogenic climate change is causing unprecedented rapid responses in marine communities, with species across many different taxonomic groups showing faster shifts in biogeographic ranges than in any other ecosystem. Spatial and temporal trends for many marine species are difficult to quantify, however, due to the lack of long-term datasets across complete geographical distributions and the occurrence of small-scale variability from both natural and anthropogenic drivers. Understanding these changes requires a multidisciplinary approach to bring together patterns identified within long-term datasets and the processes driving those patterns using biologically relevant mechanistic information to accurately attribute cause and effect. This must include likely future biological responses, and detection of the underlying mechanisms in order to scale up from the organismal level to determine how communities and ecosystems are likely to respond across a range of future climate change scenarios. Using this multidisciplinary approach will improve the use of robust science to inform the development of fit-for-purpose policy to effectively manage marine environments in this rapidly changing world.

1. INTRODUCTION

The world's oceans encompass 71% of the surface of the planet from the poles to the tropics, and have a natural, year-round, global sea temperature gradient that is evident between the warm tropical areas and the cold, polar regions. At the regional oceanographic scale, warm and cold currents also influence seawater movement and temperature trends within the oceans, including long-term, large-scale oceanographic water circulation patterns such as the Gulf Stream, transferring seawater from the east coast of the United States in a northeasterly direction across the Atlantic Ocean to the western and northwestern coastlines of the United Kingdom and Europe. Additionally, large-scale, pervasive climate patterns and modes such as the North Atlantic Oscillation (NAO), Atlantic Multidecadal Oscillation, Pacific Decadal Oscillation and the El Niño Southern Oscillation occur over multiannual time periods, affecting not only oceanic and atmospheric processes and patterns in temperature, but also precipitation and oceanic storm tracks across large areas of the globe (Hurrell, 1995). These long-term

atmospheric pressure differences have implications for the oceanography and long-term impacts on the diverse range of marine biota and ecosystems. In addition, latitudinal gradients in oceanic temperature and large-scale oceanic circulation also influence marine species and ecosystems. In the Northeast Atlantic the NAO consistently explains variation in the growth of marine fish, their abundances and assemblage compositions (Attrill and Power, 2002), while in the North Sea the NAO has been linked to changes in the biodiversity and carrying capacity of the pelagic ecosystem resulting in an abrupt regime shift (Beaugrand et al., 2008).

While there are naturally occurring short-scale weather, and longer-term environmental patterns in the marine oceanic environment, the anthropogenically driven, globally important effect of climate change is superimposed on these natural sources of variability, with warming of around 1°C in the northeast Atlantic between the 1980s and 2010s exceeding the mean global ocean warming of 0.06°C (Levitus et al., 2000; Southward et al., 2004a). In addition to the global oceans being warmed as a direct result of pervasive, human-induced greenhouse gas emissions, natural environmental events and cycles outlined above are also being altered in duration, frequency and intensity during recent decades, with anthropogenic climate change being the primary driver of these changes (IPCC, 2014).

The monitoring and understanding of oceanic provinces (biogeographic areas categorized by the differences in biogeochemical processes and biodiversity between ocean regions), cycles and the species that inhabit the global seas have long been of interest to people in both the scientific and amateur naturalist communities around the world. The wealth of available data extending back across the last two centuries stems from the long tradition of recording the natural history across natural habitats. The United Kingdom was one of the pioneering nations that instigated such studies, including many of the early investigations of the marine ecosystems that were focused on the Northeast Atlantic ocean from the late 1800s onwards (including Bergmann, 1847; Burrows et al., 2002; Crisp, 1964; Crisp and Fisher-Piette, 1959; Fischer-Piette, 1953, 1955; Fischer-Piétte, 1963; Forbes, 1853, 1858; Hutchins, 1947; Lewis, 1956, 1976, 1986; Mieszkowska et al., 2006a, 2009, 2014b; Orton, 1920; Southward and Crisp, 1954a,b; Southward et al., 2004a).

Global climate change is the largest and most pervasive stressor now acting on marine systems globally, severely and rapidly impacting marine species and ecosystems. Rapid alterations in the marine climate are forcing species to adapt to climate-driven changes, move to track the rates of climatic changes or become locally extinct, with a high degree of spatial

and temporal heterogeneity in the resultant impacts on marine communities. Such a wide spatiotemporal range of effects can only be detected through the analysis of data collected at many locations spanning large sectors of the biogeographic range of marine species, across multiple years and decades. It is fortunate that several long term, sustained observation programmes of marine life were initiated before the onset of the current period of climate change. Today's researchers can utilize these long-term time-series as resources to segregate natural and multiple sources of anthropogenically induced change in marine ecosystems (e.g. Burrows et al., 1992; Holme, 1961; Mieszkowska et al., 2009, 2014a; Simpson et al., 2011; Southward, 1967; Southward et al., 1995), and to track trends and pervasive shifts around the global oceans across decadal and century-scale timeframes.

Here we explore the value of rare, sustained observations of the marine environment, ecosystems and component species with respect to the detection of long-term trends, and shifts in biogeographic distributions of coastal benthic species across a major marine biogeographic boundary between Boreal and Lusitanian provinces in the Northeast Atlantic. Such time-series are invaluable due to their applicability for the determination of spatial and temporal heterogeneity in climate change impacts, which are of greater spatiotemporal magnitude than the majority of research and monitoring for the marine environment that only covers specific areas for a short time period. The importance of studying and recording the distribution and abundance of species across large sectors of their biogeographic distributions, and the use of sustained time-series datasets in the development of predictive modelling of future changes to marine species are discussed.

2. THE RISE OF NATURAL HISTORY AND SPECIES RECORDING

Our coastal habitats contain a wealth of biodiversity, and there has been a long history of recreational exploration of the coastal habitats across the coastal ecosystems within the Northeast Atlantic region. In the 19th century, natural history became popular and fashionable among the gentry and a new generation of amateur naturalists were born. Several books on the natural history of nearshore and intertidal habitats around the UK were published and the collection of specimens and pressing of seaweeds were pursued by many, reflecting a rich heritage of descriptive studies on British rocky shores (Burrows et al., 2014; Hawkins et al., 2010; Mieszkowska et al., 2006a; Sugden et al., 2009).

During this time, major exploratory voyages were funded by the British government to gather scientific data on a wide range of oceanic features, most notably the Challenger Expedition which set out to gather data on ocean temperatures, seawater chemistry, currents, marine life and the geology of the seafloor (Thomson and Murray, 1873–1876). This voyage resulted in the first systematic plots of currents and temperatures in the oceans and built on previous work by Maury (1855) that brought together thousands of data points on winds and currents and identified the major trade routes at the time. These UK expeditions received overwhelming support from the general public and further swelled enthusiasm for marine habitats.

The rise in interest in the natural world and success of such voyages led many to believe that closer study of the marine environment was needed and that dedicated laboratories should be established in order to facilitate this. The Marine Biological Association of the United Kingdom was established in 1884 to meet this growing need. Initially focusing on fisheries and overexploitation, several additional laboratories quickly followed suite and were established in the following years. Many amateur naturalists, who had undertaken the description of species within the marine environment, quickly became associated with these laboratories and bestowed their pioneering collections upon their institutions (e.g. Alder and Hancock collected specimens between 1845 and 1855 which are now held at the Dove Marine Laboratory and the Great North Museum: Hancock).

Museum collections such as those donated by pioneering naturalists not only serve to classify and describe the abundance of species found in coastal and marine habitats at the time but also to act as a repository of information providing data on the morphological characteristics, that can be related where historical records of physical conditions exist to environmental conditions at the time of collection. In areas where studies on benthic species are sparse and evidence for changes in the climate and its impact on species assemblages are limited, these collections can provide information regarding the functioning of ecosystems and changes in communities and geographical distributions as a response to global climate change (Wernberg et al., 2011), although such data cannot provide information on ecosystem functioning or community change as most samples were collected systematically, with only a limited part of the community being sampled during a survey.

The groundswell of enthusiasm for marine biology has not waned and with the rise of recent citizen science initiatives around the world, there has never been a greater opportunity for members of the general public to contribute to the field of ecology. Citizen science has an important role to

play in the collection of data and the building of evidence bases in ecological sciences (Dickinson et al., 2010; Roy et al., 2012). Identifying and understanding the patterns which occur at broad geographic scales are the first step in looking at natural vs anthropogenic variability and change. This requires large datasets across large spatial scales, collected for species from many taxonomic groups, with surveys across all of the seasons, for multiple years. Citizen science can contribute directly to this goal by identifying biogeographic patterns for marine species, even without aiming to understand the mechanistic drivers. Citizen science surveys can fill datagaps that exist between the few marine scientific surveys that span large geographical areas over long time periods, and help to address the urgent need to detect, track and predict the rapid effects of global climate change on marine species, communities and ecosystems (see also chapter "Recommendations for the next generation of global freshwater biological monitoring tools" by Jackson et al., in this volume). Citizen science can be complementary to additional experimental science to support emerging questions about the distribution of organisms across space and time (Conrad and Hilchey, 2011; Dickinson et al., 2010), but does not replace scientific research with respect to taxonomic expertise, quality assurance and surveyor accuracy or methodological consistency.

3. HISTORY AND DEVELOPMENT OF BIOGEOGRAPHIC RESEARCH IN THE NORTHEAST ATLANTIC

Here we outline some of the major scientific developments and advances in knowledge that facilitated the field of marine biogeography within the Northeast Atlantic since the start of systematic scientific and recording in the 1800s, and served as novel examples for the rest of the world's oceans.

The development of the field of marine biogeography in the late 19th century is evidenced in the British scientist Forbes' pioneering biogeographical map published in 1858, where he mapped the boundary between the cold-temperate Boreal and warm-temperate Lusitanian regions bisecting the UK, and related these to geographical changes (Forbes, 1858). Forbes' observations that species were grouped according to these areas, with distributional limits occurring in the vicinity of the transition zone are still broadly applicable today.

Forbes made three observations of lasting value to marine research: (1) each zoogeographic province is an area where there was a 'special manifestation of creative power' (a geographic location where many species evolved and dispersed from), and the animals originally formed there can become

mixed with emigrants from other provinces; (2) each species was created only once, and individuals tend to migrate outwards from their centre of origin to new locations (the abundant centre hypothesis) and (3) provinces must, to be understood, be traced back, like species, to their origins in past time (track their evolutionary history). These points are of value to phylogeographic studies and are useful tools for understanding how climate change will impact a specific species with respect to their thermal evolutionary origins.

The American phycologist Setchell (1915) proposed a series of nine biogeographic zones bounded by summer temperatures, based on the historical background of regional terrestrial faunistics and floristics. These zones he then demarcated into subzones on the basis of the winter temperatures within them to explain the distribution of marine macroalgae. This viewpoint was to be debated in later decades, when this expectation of a single system of zonation to summarize the empirical diversity of biological distributions was disputed, and considered inappropriate as an interpretive summary for marine species distributions (Hutchins, 1947). This heuristic tool can aid our understanding of large-scale trends or shifts in the biogeographic distribution of species; however, it has limited applications with respect to the prediction of climate change impacts due to the coarse spatiotemporal scale of the zonation scheme to classify biogeographic provinces.

Building on the ideas presented by Forbes, the Swedish scientist Ekman undertook the huge task of analysing all of the pertinent literature available on marine animal distribution at that time, leading to the publication of his book *Tiergeographie des Meeres* (Ekman, 1935). This was the first systematic treatise on historical marine biology to be published (Kafanov, 2006) and was followed by a revised English edition, *Zoogeography of the Sea* (Ekman and Palmer, 1953). Ekman and Palmer (1953) considered the marine world to be composed of a series of large regions or subregions. For the continental shelf, they described regions located in warm, temperate and polar waters; their separation by zoogeographic barriers and their endemism. He proposed a new, qualitative 'Eckman Index' modified from the Jackard Similarity Index, Pesenko (1982) that has served as the basis for a continually developing topic, comparing the similarity and diversity of species within a sample, that is still relevant in modern scientific research today. The American researcher Briggs (1974) divided the continental shelf further, into a series of large biogeographic regions that, in turn, contained smaller provinces, defined on the basis of endemism (Briggs and Bowen, 2013).

Today, several versions of global marine classifications exist, dividing the world's oceans into between 54 and 62 marine biogeographic provinces,

providing large-scale delineations of major faunistic regions (e.g. Berlanger et al., 2012; Briggs and Bowen, 2013; Spalding et al., 2007; VLIZ, 2009). These are based on the wealth of knowledge and data collected throughout the modern history of marine science, combining long-term time-series, field-based records and observations, experimental research, remote sensed oceanographic and biological data, and understanding of the biogeographic distributions and abundances of marine algae, invertebrates and vertebrates. Differences in the exact number of provinces can be traced back to the specific faunal list and species groups with which each classification was determined, however, they are still in major agreement with each other at the global scale. With these data and biogeographic classifications, the natural and anthropogenic factors that set and change the distributions of marine species across a range of spatial and temporal scales can be studied at the ocean-basin scale. Such coarse classifications are a useful starting point from which to track the movement of the range edges of species that are located at the edges of these biogeographic provinces by the comparison of current distributions to historical locations. Such a large-scale approach, however, does not capture the patterns of species distributions, including the latitudinal variation in range boundaries across marine taxa, the smaller scale variation between populations within the biogeographic range, the biological processes shaping the range edges and the overlaps in distributions of species originating in neighbouring but differing biogeographic provinces that are known to occur. Such data are essential in order to accurately forecast future changes to the biogeographic distributions of marine species arising from pervasive anthropogenic climate change against the background of long-term natural evolution and changes to marine ecosystems.

4. PATTERNS OF CHANGE ACROSS THE BOREAL–LUSITANIAN BIOGEOGRAPHIC BREAKPOINT IN THE NORTHEAST ATLANTIC

A wealth of small-scale, species or taxa-specific studies date back through the 1900s and late 1800s for intertidal and shallow subtidal benthic systems and species around the English and French coastlines, with occasional studies along the Atlantic coastlines of Spain and Portugal. Many surveys in England and Wales were completed by a small group of researchers at the Marine Biological Association in Plymouth, Robin Hood's Bay Marine Laboratory and collaborative universities (Boalch, 1987; Crisp and Southward, 1958; Lewis, 1986; Russell, 1973; Southward, 1967) in the early to mid-1900s (Southward et al., 2004a, for review).

French surveys were predominantly carried out by researchers based at, or with links to the Station Biologique de Roscoff, which was founded in 1877. These field campaigns were predominantly focused on the English Channel and Brittany region (Fig. 1; e.g. Ancellin et al., 1969; Audouin and Milne-Edwards, 1832; Beauchamp, 1914; Crisp and Fisher-Piette, 1959; Davy de Virville, 1940; Fischer-Piette, 1932, 1934, 1936; Fischer-Piette and Gaillard, 1956; Gaillard, 1965; Plessis, 1961; Prenant, 1927). Most were isolated studies with restricted geographical or taxonomic focus, different recording methodologies and lack of cross-calibration between surveyors working on the same species or families. The lack of integration

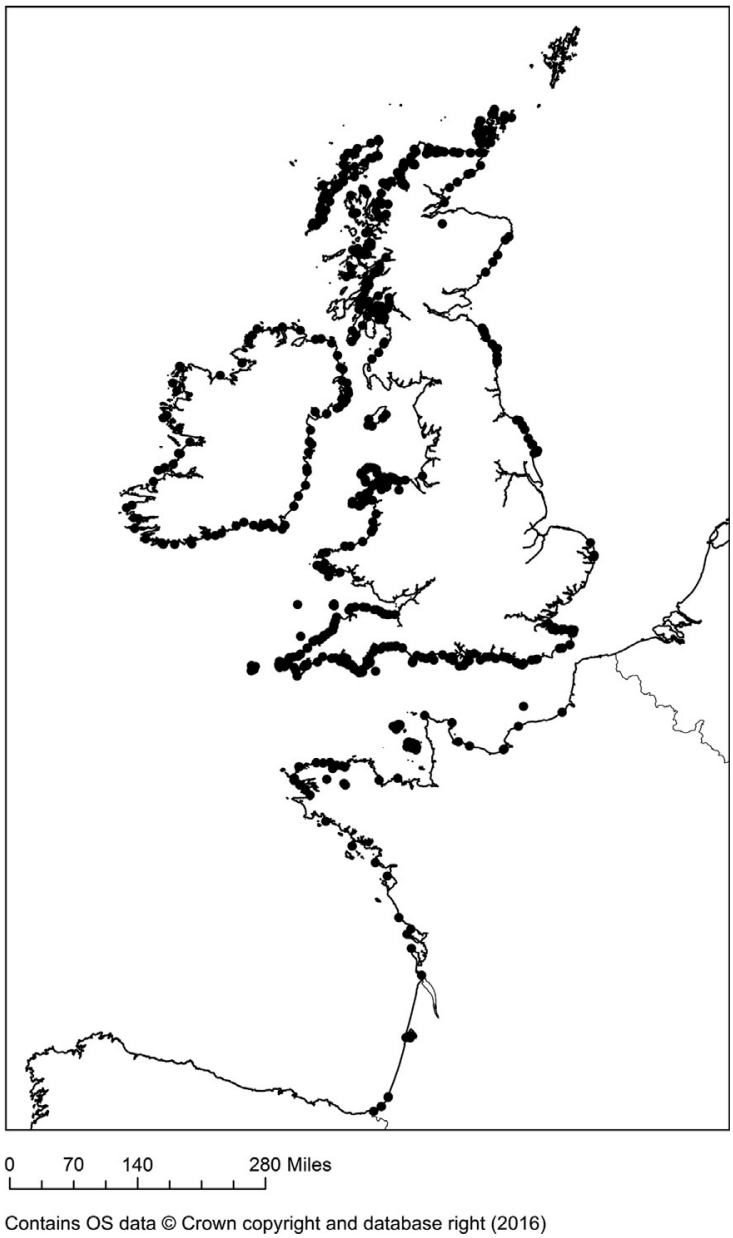

Fig. 1 Map of the UK and France showing the MarClim long-term survey locations.

or use of common methodologies between these studies prevents the quantitative assessments of range shifts, and metaanalyses of community-level changes difficult to undertake due to the lack of standard data collection techniques.

Some continuity between surveyors exists over this time period, with Fischer-Piétte completing broadscale surveys of rocky intertidal species along the coastlines of France, Spain and Portugal in the 1950s (Fischer-Piette, 1953, 1955, 1958; Fischer-Piétte, 1963), and a survey of the French Atlantic coastline with Crisp (Crisp and Fisher-Piette, 1959), who also carried out the UK surveys with Southward (Crisp and Southward, 1958; Orton, 1920; Southward and Crisp, 1954b). The extensive time-series observations for coastal systems in the northeast Atlantic dating back several decades has facilitated research into the detection and quantification of species range shifts both at the Boreal/Lusitanian transition zone bisecting the UK and the Atlantic coastline of Europe (Lima et al., 2007a,b; Mieszkowska et al., 2006b, 2014b).

Multidecadal-scale shifts in species distributions, and the resultant changes to community composition at benthic coastal survey sites within the region of the Boreal–Lusitanean biogeographic marine boundary in the Northeast Atlantic have been studied using these comprehensive datasets with extensive geographic coverage spanning over four degrees of latitude for key structural and functional species of rocky intertidal invertebrates and macroalgae.

For the Galician coast, species distributions for kelps were compiled from a range of studies spanning the 1920s to 2000s and along the Portuguese coast, observational data (presence/absence) were available for kelps and trends assessed by comparing literature records reporting the presence of the species in the 1960s (Ardré, 1970) and observational data in 2008/2010 (Assis et al., 2009, 2013).

Differences between distributions of animals on the north and south coasts of the channel are less conspicuous than those between the east and west basins. There is a clearly marked east-to-west trend in the distributions of many of the animals and plants which has been described. In nearly all such species, not only is the general trend from east to west the same, but also the range and even the detailed features show that a remarkable similarity exists between the British and French coasts.

The differences that exist are due to the presence of more southern forms on the French coast (Crisp and Southward, 1958). In the 1950s, *Gibbula umbilicalis* and *Littorina neritoides* had a greater range eastward on the French

side: and *Bifurcaria tuberculata*, *Laminaria ochroleuca* and *Gibbula magus* were generally more abundant in France. Several species were found exclusively or almost exclusively on the French side, such as *Gibbula pennanti*, *Haliotis tuberculata*, *Paracentrotus lividus*, and also species not included in the present survey such as *Pollicipes cornucopia* (now *Pollicipes pollicipes*) and *Pachygrapsus marmoratus*, which was at one time present in the Roscoff area. The only species which appeared to be more abundant on the British coast was *Chthamalus stellatus* (Crisp and Southward, 1958).

The distribution and density/abundance of individual native kelp species are declining in southern European areas (Northwestern Iberian Peninsula, Gulf of Biscay and Mediterranean Sea), with the exception of the Southern Iberian Peninsula where no trends were observed (Araújo, pers. comm.). French experts reported a decreasing trend or stability of *Laminaria hyperborea* beds in Brittany and a general decrease in *Laminaria digitata* and *Saccharina latissima* in Northern France (eastern English Channel and Dover Strait), even if some areas were characterized by a relative stable kelp distribution, such as Iroise/Ushant Sea and North Brittany (Billot et al., 2003). German experts reported an increase in *L. hyperborea* in the southern North Sea and concomitant slight decline of *S. latissima*.

In central Europe, trends of the most abundant kelp species vary according to species identity and geographical area. Kelp abundances around the UK have shown a shift towards increasing abundance of Lusitanian species including *Sacchoriza polyschides* and *Laminaria ochroleucha* in recent decades in response to warming of the marine climate (Brodie et al., 2014; Mieszkowska et al., 2006b; Smale et al., 2015). Boreal kelps have not shown a significant decline in abundance to date, however, they are predicted to decline in abundance and undergo range retractions with continued climate change (Brodie et al., 2014). A metaanalysis of intertidal brown macroalgae around the UK coastline found regional differences in abundance trends, with declines in the southern region, but no change or increases in central and northern regions of the UK (Yesson et al., 2015).

Around the coast of France, kelp abundances vary independently of the latitude. Brittany constitutes a mosaic of contrasting conditions, with the western and northwestern regions being colder and less affected by climate change than the other three regions (Derrien-Courtel et al., 2013; Gallon et al., 2014). Signs of maladaptive response (alteration of meiosis) of *L. digitata* at its southern edge of its distribution (southern Brittany) became apparent where genetic diversity has declined (Oppliger et al., 2014). Such a response means that this European kelp species is at risk of local extinction as

predicted by ecological niche models under global change scenarios (Assis et al., 2015; Raybaud et al., 2013).

In the Iberian Peninsula, quantitative data are scarce for most of the species but in the southwest of Portugal and along the Bay of Biscay, a trend of decreasing abundance was verified for *S. polyschides*, *L. hyperborea* and *L. ochroleuca*. These results are in accordance with recent publications reporting on range contractions and/or changes in abundance in recent years, at the southern and eastern distributional ranges of these species (Assis et al., 2013, 2015; Diez et al., 2012; Fernández, 2011; Martinez et al., 2015; Voerman et al., 2013). Global warming was the main driver of changes in kelp abundance identified for this region which is in agreement with recent studies relating the recent retreat in kelp distribution with the global trend of increasing sea surface temperature (Bartsch et al., 2012; Diez et al., 2012; Voerman et al., 2013) and with modelling approaches (Bartsch et al., 2012).

Comparative species distribution modelling found that subtidal red species in the English Channel spanning the biogeographic breakpoint showed differing responses to increased sea temperature between the survey periods 1992–98 and 2010–12. A decrease in the distribution of most species occurred in the three easterly sectors, whereas the western and northwestern Brittany sectors showed more stability and were proposed as potential future refuges for this phylum under future climate change (Gallon et al., 2014). Subtidal algal communities around the Iberian Peninsula and the Canary Islands have also been documented to be changing in composition to favour more Mediterranean species (Martinez et al., 2015).

5. FACTORS SETTING BIOGEOGRAPHIC RANGE LIMITS

5.1 Environmental Conditions

The biogeographical investigations that were initiated in the late 1800s and early 1900s on the species present in studies spanning geographical regions were additionally able to generate a new awareness of the role that the environment played in setting both (in intertidal habitats) vertical and latitudinal boundaries (Appellof, 1912; Couthouy, 1844; Dana, 1890; Orton, 1920; Parr, 1933; Runnström, 1929, 1936; Schmidt, 1909; Setchell, 1893, 1915, 1917, 1920a,b, 1922). Hutchins' seminal paper (Hutchins, 1947) expanded further on this concept, proposing biogeographic provinces across the entire northern hemisphere, based on the distribution of coastal species. He proposed two general theories on the factors setting range limits that are

still widely acknowledged today: first, that the distributional range edges for a species will occur where seasonal temperatures become too extreme for the survival of individuals, such as mortality due to cold winter temperature, or an inability to survive hot summer temperatures. Second, critical temperatures for the completion of life cycle stages—such as a trigger to induce spawning, and growing seasons of adequate duration as well as intensity—may set range boundaries via nonlethal, biological, mechanistic responses of individuals experiencing the environmental thermal regime. The effects of temperature acting on physiological mechanisms can be seen on a local scale at the population level, and such changes have been shown contribute to regional-scale variation in species distributions and range limits. Temporary populations can exist beyond range edges, however, they do not become established, either due to rare extremes or insufficient larval supply. Thus, distributions may be limited both towards the poles and towards the equator by either lethal or sublethal thermal tolerances or requirements, which can be related to summer and/or winter seasonal conditions (Hutchins, 1947). The broad pattern observed in species distributions for coastal marine systems along the latitudinal extent of European rocky shores was observed to be related to environmental temperature, but also to environmental gradients in physical factors such as water coverage, wave exposure, air and sea temperature and irradiance (Connell, 1975).

Temperature is a primary driver setting the distribution of marine species globally (Atkinson et al., 1987; Cain, 1944; Parmesan and Yohe, 2003; Stenseth et al., 2002). Climate is a pervasive influence at all levels of organization in biotic systems because of temperature-dependent processes from enzyme reactions through to ecosystems, and the locations of range limits for marine species have been linked to the boundaries between adjacent marine biogeographic provinces via seasonal mean sea surface temperature isotherms (van den Hoek, 1982).

5.2 Biological Processes

In addition to the geographical factors that set biogeographic ranges, all species are also subject to controls on their distribution by the biological processes that govern an organism's ability to tolerate environmental and physical conditions. Survival, reproduction and dispersal are fundamental biological processes determining where an organism and thus populations will become established and maintained. In addition, the tolerance of a species to environmental conditions will have profound effects on the extent

and location of the distributional range. Additional biological processes including metabolism and ontogeny processes, and the plasticity of the underlying mechanisms all contribute to the physiological performance of an organism. Geographic distributions are thus a function of a range of morphological and physiological adaptations of individual organisms, characteristics acquired through the process of natural selection.

5.3 Ecological Factors

Further complicating the determination of the driving factors setting species distributions are ecological factors, such as interactions between species. A species invading a new location will encounter other species with which it has never had contact, leading to the potential for competitive, predatory or compensatory interactions. When these adaptations confer a positive effect for an organism, it will survive and have the opportunity to proliferate in this new location, whereas in locations where such adaptations have a negative impact, the distribution will be constrained, ultimately causing a distributional limit or gap in the distributional range.

5.4 Defining the Habitat of a Species

The role of biotic vs abiotic factors in determining the distribution and abundance of marine animals, and whether the importance of the different factors and their significance for population density varied across a species' range, were two important issues that were further studied over the second half of the 20th century by researchers on both sides of the North Atlantic (Andrewartha and Birch, 1954; Crisp and Southward, 1958; Cushing and Dickson, 1976; Edwards et al., 2001; Nicholson, 1954; Southward, 1995; Southward et al., 1988). The habitat of any species defines both the abiotic (environmental and physical) and biotic (biological and ecological) parameters that promote survival of an organism, and their variation across space and time at the biogeographic scale determines the distributional range of a species.

Early into the development of biogeographic studies on the marine environment, researchers focusing on North Atlantic coastal marine ecosystems identified temporal and geographical patterns in the abundances of benthic and pelagic species at sites where repeated surveys were carried out. They also began to discuss environmental 'features' of habitats that were potentially setting geographical distributions for coastal marine species, with sea

and air temperature, salinity, nutrients and hydrodynamics that comprised a habitat being proposed as the likely drivers (Crisp and Southward, 1958).

The abundances of cooccurring species of cold-temperate, high-latitude and warm-temperate, mid-latitude species reflected fluctuations between a warm period in the 1950s and a cooler phase across the 1960s and 1970s (Southward et al., 2004a, for review). These changes correlated with natural cycles in oceanic conditions (Cushing and Dickson, 1976; Russell et al., 1971; Southward, 1991) and the understanding of the role of climate, and how changes in environmental temperature could alter species distributions.

Much of this early work was carried out in the UK, providing a wealth of data on temporal fluctuations in population abundances for coastal species in the vicinity of the major marine boundary between Boreal and Lusitanian provinces. Investigations on the distribution of barnacles around the UK coastline in the 1950s prompted the initiation of the first repeated, broad-scale surveys of the abundance and distribution of invertebrates and macro-algae around the coastlines of Ireland and the English and French sides of the English Channel by Crisp and Southward (1958) and Southward and Crisp (1954a). Complementary studies were carried out around the UK by J.R. Lewis and colleagues at the Robin Hood's Bay Laboratory in the northeast of England during the 1980s (Lewis, 1976, 1986; Lewis et al., 1982). The data from these studies were collated, and resurveys started at The Marine Biological Association of the UK from 2001, and form one of the most spatiotemporally extensive intertidal time-series in the world today (Mieszkowska et al., 2006a, 2014b; Southward et al., 2004a).

Van den Hoek (1982) and Breeman (1988) mapped broadscale distributions of macroalgae across the North Atlantic. They noted that high-latitude range edges occurred close to winter sea surface temperature isotherms corresponding to species' thermal minima, and low-latitude limits were located where the highest summer temperatures correlated with upper thermotolerance limits. The distributional limits of most algal species in this oceanographic region seemed to be set by sublethal effects of temperature via the prevention of growth and/or reproduction, rather than by lethal effects. Moreover, these sublethal effects would act on species of colder, Boreal and cold-temperate species at different times to warm-temperate 'warm water' species. The poleward expansion of most warm water species would be limited by the absence of suitable high temperatures during the summer, while the equatorial range extension of coldwater species would be hindered by the effects of warm winters. More recent studies of the status, distribution

and abundance of kelps along the seaboards of the Northeastern Atlantic have shown a general trend that supports these theories at the continental scale, with decreasing abundance of some native kelp species at their southern distributional range limits and increasing abundance in northern, higher latitude sectors of their distribution (Araújo et al., 2016).

The temporal frequency of observations for such time-series were mostly seasonal or annual, providing long-term insights into trends or oscillations of marine benthic species at the decadal scale, but being of insufficient temporal resolution to show shorter term and/or small spatial scale events, and natural stochasticity within marine systems. The general theory of the distributions of coastal marine species shifting to higher latitudes in response to chronic warming of the global oceans did not account for extreme, shorter term events such as in 1962/3 in the UK, however, where an unusually cold winter caused the rocky intertidal zone across most of Wales to freeze over, resulting in the contraction of the poleward range limits of many intertidal ectothermic species of Lusitanian biogeographic origins by hundreds of kilometres to lower, warmer latitudes (Crisp, 1964). The range limits did not reextend to similar latitudes until after several decades of warmer climatic conditions and no severe winter seasonal thermal events (Mieszkowska et al., 2006a).

The accumulated knowledge and scientific understanding from these biogeographic scale, field-based studies of the distribution of marine species spanning the 20th century has provided much of the evidence for the movement of species ranges during periods of both cooler, and the current warming of the global climate (Mieszkowska et al., 2014a,b; Southward, 1995). Most of the datasets from sustained observations time-series have been correlated with sea temperature to establish links between ongoing climate change and the geographic patterns of impacts on marine ecosystems or species (Crisp and Fisher-Piette, 1959; Crisp and Southward, 1958; Cushing and Dickson, 1976; Fischer-Piette, 1955, 1958; Forbes, 1858; Southward, 1963, 1967; Southward et al., 2004b). This approach has advanced the knowledge of how benthic marine algae, invertebrates and vertebrates have, and are likely to respond to climate change; however, correlative analyses and models are unable to determine causal drivers or mechanisms underpinning biogeographic shifts. In addition, correlative approaches including species distribution models (SDMs) assume that species are at equilibrium with their environments, and that environmental gradients have been adequately sampled, are thus unable to accurately forecast future changes in species distributions in novel climates that have not been experienced in the history of

any extant marine species (Elith and Leathwick, 2009). Correlative SDMs and metaanalyses have been useful for demonstrating broadscale trends in how ecological systems are responding to climate change and are useful frameworks with which to estimate the magnitude of future impacts (Helmuth et al., 2015a).

The environmental factors controlling the abundance and distribution of species have long been of interest to ecologists. Nevertheless, better understanding is required of the biological mechanisms enabling species to survive and the environmental drivers of these processes in light of the current period of global warming (Holbrook et al., 1997; Lodge, 1993; Lubchenco et al., 1993; Mooney, 1991; Mooney et al., 1993). Biogeographical time-series, combined with more recent, targeted, experimental research to determine the biological mechanisms by which species are responding to environmental temperatures have advanced our understanding of which environmental factors, and biological responses set biogeographical range limits for marine species inhabiting the Northeast Atlantic coastal seas. Climate impacts research is undergoing a paradigm shift facilitated by emergent physiological measurement technologies and newly available environmental data at microclimatic scales relevant to individual organisms and populations. With the development of modern experimental, molecular and mathematical techniques in recent decades, the biological processes and mechanisms underpinning species-specific responses to both range limits set by natural environmental conditions and alterations to biogeographic distributions as a direct or indirect result of anthropogenic climate change are now being quantitatively documented, and forecasts of future change statistically modelled (see Section 8 for further information).

6. LONG-TERM TIME-SERIES FOR BENTHIC ECOSYSTEMS IN THE NORTHEAST ATLANTIC AND REGIONAL SEAS

6.1 Marine Biodiversity and Climate Change: MarClim

The value of repeated observations of biological and environmental parameters was first recognized in the mid-1950s with the establishment of broadscale surveys around the coastal habitats of the UK to investigate the movement of invertebrates at their range edges (Lewis, 1976). Southward (1980) stated that '*The need for sustained biological monitoring and development of methods of prediction is obvious*' (Southward, 1980; Southward et al., 1995), really highlighting this need for sustained observations.

Surveys of the rocky intertidal zone conducted around the coastlines of France and England during the 1950s and sporadically throughout the 1960s and 1970s (Crisp and Fisher-Piette, 1959; Crisp and Southward, 1958; Southward and Crisp, 1954a), the 1980s (Hawkins, unpublished data) and 2000–15 (Mieszkowska et al., 2006a, 2014b) have been combined by the MarClim Project, run by the Marine Biological Association of the UK. This combined dataset represents the most spatiotemporally extensive time-series for intertidal systems globally and continues the annual recording of species abundances and distributions at 120 time-series sites to date (Mieszkowska et al., 2014b). The data were collected by trained surveyors, experienced in rocky intertidal taxonomic identification, using the same methodology for all surveys across the decades. Each surveyor trained and cross-calibrated the next generation of surveyors, ensuring comparability between data from Crisp and Southward to Hawkins and Mieszkowska, then Sugden, all of whom were cross-calibrated with at least two of these surveyors in the field.

Species abundances at each site were collected using the categorical ACFOR scale developed by Crisp and Southward (1958), whereby species were assigned a category of either abundant, common, frequent, occasional, rare or not seen (absent) based on the percentage cover for sessile species and the number of individuals per m^2 for mobile species. This methodology has been shown to be an accurate means of assessing both abundance and changes in abundance (Mieszkowska et al., 2006a) and is amenable to analysis using modern statistical methodologies including density-structured dynamic species distribution modelling (Mieszkowska et al., 2014b) and hierarchical ANOVA at nested spatial scales (Burrows et al., 2009).

The data collected to form this time-series are now being utilized to inform both UK and EU policy, most notably as an indicator of Good Environmental Status for the Marine Strategy Framework Directive. It has been analysed to develop indicators for Descriptor 1 (Biological diversity is maintained. Quality and occurrence of habitats and distribution and abundance of species are in line with prevailing physiographic, geographic and climatic conditions) and Descriptor 2 (nonindigenous species introduced by human activities are at levels that do not adversely alter the ecosystems) (Burrows et al., 2014). This reinforces the need for large spatial and temporally extensive datasets not only to ascertain the biological mechanisms driving the patterns of change but also to determine the impacts of anthropogenic change in order that it can be appropriately managed through the creation of fit-for-purpose legislation based on robust scientific techniques.

6.2 European Kelp Forests

Kelp forests along the North Atlantic coastlines of Europe and the UK support complex coastal food webs via the provision of habitat, primary production, detrital resources and carbon export to subtidal soft sediment systems (Araújo et al., 2016; Chung et al., 2013; Krumhansl and Scheibling, 2012). The most extensive sustained observations have been carried out in the intertidal or shallow subtidal coastal habitats of Norway, France and the UK, although the data are limited in their vertical and geographical coverage of kelp forests (Araújo et al., 2016). The available data show that there has been very little shift in dominance between kelp species of cold Boreal, warm Lusitanian and invasive biogeographic origins within communities located in the low eulittoral/infralittoral along the coastal regions from Norway, south to Portugal. In subtidal areas, there has been an almost complete loss of native Boreal, cold water species along the mainland coast of Europe. This has resulted in an epibiotic community 10 times less rich in biodiversity than seen supported by native colder water kelps that provide large complex structures (Brattegard and Holthe, 2001; Breuer and Schramm, 1988; Brodie et al., 2014; Smale et al., 2013). Boreal kelps have not declined in abundance or distribution around the UK coastline with the exception of *Alaria esculenta* (Greville) that has undergone a retraction of the southern range limit in southwest England (Mieszkowska et al., 2006a; Smale et al., 2013). The Lusitanian kelp *S. polyschides* has shown extensions of the northern distributional limit around the UK during the 2000s, however, between 2010 and 2014 the abundance of all Lusitanian kelps declined at MarClim long-term survey sites around the coastlines of England and Wales (Mieszkowska, 2015a,b; Mieszkowska et al., 2014a,b). These time-series data suggest that geographical limits and survivorship are based on a species thermotolerance to extreme winter temperatures.

6.3 North Sea Soft Sediment Benthos

Benthic sediment habitats have been investigated in the North Sea since the 1960s. The data collected at these stations have been used to investigate multidecadal dynamics in the North Sea ecosystem. Patterns have been established between the abundance of zooplankton and the abundance of benthos and linked to these decadal periods of warming and cooling (Frid et al., 2009). Furthermore, these climatic oscillations are thought to drive changes in the benthic assemblages and in some instances extirpation of species in the central North Sea (Robinson and Frid, 2008).

It is proposed that despite this climate forcing within the ecosystem, normal functioning can be maintained over time, with aperiodic disruption under some conditions. Alterations to affect trait composition occurred when taxonomic composition shifted at the same time at both time-series stations in the central North Sea. This event coincided with the North Sea climatic regime shift (Beaugrand, 2004), and therefore implied alteration to benthic functioning may have been driven by broadscale hydroclimatic forcing or the associated changes to the North Sea ecosystem. The community composition of plankton changed around this time in 1987 (Beaugrand, 2004) and detrital flux to the seabed surrounding the stations was estimated to be particularly low during this period (Buchanan, 1993). It is therefore suggested that climatic variability can cause temporary changes to benthic functioning, even with systems exhibiting long-term functional stability (Frid and Caswell, 2015; Neumann and Kroncke, 2011).

Similar patterns of functional change and recovery have been reported for epifauna responding to a cold winter in the German Bight (Neumann and Kroncke, 2011) and macrofauna responding to hypoxia events over a 19-year period at a site in the southwestern Baltic Sea (Gogina et al., 2014). Benthic invertebrate communities have also been shown to exhibit a level of seasonal stability in trait expression, despite taxonomic composition being highly variable on this seasonal timescale (Beche et al., 2006; Munari, 2013); while recent analysis suggests similar patterns emerge over a period of millennia (Caswell and Frid, 2013; Frid and Caswell, 2015). Substitutions of characteristically similar benthic species may therefore occur widely and across multiple temporal scales acting to conserve ecological functioning (Frid and Caswell, 2015).

7. OBSERVED CHANGES IN THE PHYSICAL ENVIRONMENT

Anthropogenic climate change has been altering the temperature of the world's atmosphere and oceans for several decades, with persistent alterations in the global climate recorded since the early 1980s (IPCC, 2014). Records dating back over a century show how the global annual temperature has responded to the release of greenhouse gases into the atmosphere as a result of human activities, with surface temperatures increasing at an average rate of 0.07°C per decade since 1880, and at an average rate of 0.17°C (0.31°F) per decade since 1970 (IPCC, 2014). Detailed analyses of long-term increases in global sea surface temperatures have revealed that

this warming has been seasonally consistent across the second half of the 20th and start of the 21st centuries, with increases in temperature most pronounced in the winter months with temperatures increasing on average by 1.5°C over the past 50 years (IPCC, 2014). This warming has caused many sessile and mobile marine species to shift their range limits northwards towards cooler marine environments matching the observed rate of climate change (Mieszkowska et al., 2006a, 2014a). The record warmth in the global oceans has been a major contribution to this increase in global surface temperatures, with the average annual temperature for global ocean surfaces being 0.74°C higher than the 20th century average (NOAA, 2016).

The recognition that this unprecedented rate of warming would affect the survival of life on earth initiated a global research effort at the end of the 20th century to document and track climate change within the world's oceans and associated climatic impacts on the distributions of both marine and terrestrial species. Ecological theory indicated that climate impacts would likely be first manifest at the distributional range limits for many species, where organisms were already living close to thermal tolerance limits latitudes (Helmuth et al., 2006; Hughes, 2000; Parmesan and Yohe, 2003). This would result in retractions of low-latitude range limits in warmer environmental regimes, and extensions of the high-latitude range edges where colder thermal environments were increasing to more thermally tolerable values, causing a polewards shift of biogeographic ranges to higher, cooler latitudes. As these range limits are often located close to major biogeographic boundaries, these regions were proposed in the early days of marine climate impacts research as likely 'hotspots' for changes to marine biodiversity.

New analyses and advanced modelling of marine thermal data show that shifts in the thermal environment have differed across the global oceans since the onset of global warming, with resultant geographically varying rates in the velocity of climate change (the geographic shift of sea surface isotherms over time) (Burrows et al., 2011; http://www.noaa.gov/climate). In addition to these temporal inconsistencies in warming there is high spatial and temporal heterogeneity in the velocity of this change (Lima and Wethey, 2012) due to the shallow mixed layer depth at tropical latitudes vs the deep mixed layer in polar regions (Schneider and Thompson, 1981). Significant changes in regional oceanic temperature can be detected within 10 years in the tropics, but can take an order of magnitude longer to be observed at the poles (Schneider and Thompson, 1981; Washington and Meehl, 1989). The temperate seas of the Northeast Atlantic region have experienced phases of warming (e.g. 1920s to 1950s) and cooling (early 1960s to mid-1980s)

throughout the 20th century (Southward, 1980; Southward and Butler, 1972), with a 'hiatus' in warming being evident for the first half of the 2010s (IPCC, 2014). The North Atlantic has shown some of the largest increases in sea surface temperatures globally (Hawkins et al., 2003; Scharf et al., 2004; Southward et al., 2004a; Woehrlings et al., 2005) which is twice the rate of any previous warming event on record (Mann et al., 1998, 1999). In the western English Channel off Plymouth, a 1°C increase in mean sea surface temperature has occurred since 1990. This increase exceeds any other change recorded over the past 100 years (Hawkins et al., 2003) and is most apparent in winter months. The rate of warming cannot be predicted with certainty but models based on medium–high CO_2 emissions scenarios indicate that sea surface temperatures around Britain will increase by between 0.5 and 5°C by 2080 (Hulme et al., 2002).

In addition to increases in global surface temperatures, increased emissions of CO_2 into the global atmosphere as a result of anthropogenic activities are resulting in increased ocean acidification (Gattuso et al., 2015; IPCC, 2014; Schiermeir, 2004; Turley et al., 2004). Rising atmospheric CO_2 is tempered by oceanic uptake as are rising global temperatures. This uptake of CO_2 leads to reductions in the pH of ocean waters and alterations in fundamental chemical balance. The acidification of surface waters is well documented (Feely et al., 2008) and leads to lower $CaCO_3$ saturation (Caldeira and Wickett, 2003). Changes in ocean pH are seen as a threat to marine biota as many utilize $CaCO_3$ is the calcification of hard structures (Orr et al., 2005; Smith and Buddermeier, 1992). Emergent research is demonstrating that the biological effects are far more complex than the limitation of calcification levels alone and can include alterations to immune, growth and reproductive systems (Bibby et al., 2008; Gazeau et al., 2010; Kroeker et al., 2013; Kurihara, 2008). There is high variability in the vulnerability of different species to ocean acidification, with some species showing positive responses to increased pCO_2 (Kroeker et al., 2010). This leads to a complex set of interactions acting on marine organisms whose responses may vary considerably from species to species, however, the biological mechanisms involved, and the extent of impacts at the suborganismal level is still largely unknown, and much further research is required to accurately determine the biological responses of marine species to ocean acidification.

Temperature is a pervasive influence at all levels of organization in biotic systems from the temperature-dependent enzyme reactions through to the structure and functioning of ecosystems (Atkinson et al., 1987; Cain, 1944; Parmesan and Yohe, 2003; Stenseth, 2008). Concerns regarding the

responses of natural systems changes in environmental temperature due to climate change in recent decades have prompted a vast research effort to assess and understand the type and extent of responses that have already occurred, and to develop the ability to predict future changes as global warming continues. Marine species have been shown to track the local climate velocities, demonstrating the need for a thorough understanding of both the spatiotemporal variation in climate change, and the individual, population and species-level responses to such change (Pinsky et al., 2013).

Climate change may affect species via such long-term, low-amplitude directional shifts in temperature (Russell, 1973; Southward, 1963, 1991), but also by acute, short-term events including changes in temperature, droughts and flooding which have spatially extensive impacts that last for decades (Bailey, 1955; Crisp, 1964; Hawkins and Holyoak, 1998; Huntsman, 1946; Mattson and Haack, 1987; Smale and Wernberg, 2013).

Extensive disruptions of most terrestrial (Parmesan and Yohe, 2003; Peters and Lovejoy, 1992; Walther et al., 2002) and marine (Fields et al., 1993; Graus and MacIntyre, 1998; Hoegh-Guldberg, 1999; Holbrook et al., 1997; Peters and Lovejoy, 1992; Precht and Aronson, 2004; Ray et al., 1992; Schneider, 1993; Vitousek, 1994; Vitousek et al., 1996) ecological assemblages are expected to continue during the 21st century as species are continually forced to move, adapt or suffer extirpation (Holt, 1990) in response to the unprecedented levels of global climate change predicted by global climate models (Houghton et al., 1995, 2001).

8. IMPACTS OF CLIMATE CHANGE ON INTERTIDAL BENTHIC SPECIES

Intertidal ecosystems are one of the most extensively studied marine habitats due to their easy access, and diurnal exposure to surveyors due to the tidal cycle. The ecology and biology of the species and communities within these habitats are also well understood, and underlie much of the existing knowledge and theories that are used across ecological research and teaching today. They are familiar systems to scientific, governmental and lay audiences and provide important insights into the effects of climate change that can be disseminated to nonspecialist audiences and decision makers around the globe.

Intertidal ecosystems differ from other marine environments, however, because they exhibit enormous thermal variability in time and space, with most of the variation occurring within and because of diurnal and tidal cycles

(Helmuth et al., 2002). Consequently, average temperature estimates, even at the very small spatial scale of an individual habitat, do not accurately encapsulate the habitat thermal heterogeneity and total range of body temperatures that organisms experience on a regular basis, which can be much higher than the temperature of the surrounding air, even under moderate levels of solar radiation (Helmuth et al., 2002; Kearney et al., 2012, 2013; Marshall et al., 2010). In these spatially and temporally heterogeneous intertidal thermal environments, with multiple daily changes in tidal cover, wind, precipitation and solar radiation, selection associated with temperature extremes is likely to play a major role, and behavioural thermoregulation may constitute a crucial strategy to ameliorating the impact of stressful temperatures (Bonebrake and Deutsch, 2012; Kearney et al., 2009, 2012). The detection of responses of benthic species to climate change, and a comprehensive understanding of the biological mechanisms underpinning shifts in distributional ranges must therefore combine large scale, long-term recording of the abundance and biogeographic ranges with experimental physiological research to populate biophysical models capable of predicting biologically realistic predictions of future responses of species to climate change.

8.1 Biogeographic Range Shifts

Species-specific responses can be highly variable, raising concerns regarding broadscale generalizations and metaanalyses of polewards range shifts. Range shifts are occurring faster in the marine environment than in terrestrial ecosystems (Poloczanska et al., 2013). This likely to be due to a combination of factors including: greater connectivity within the marine system (Menge, 2000; Thorson, 1950), less habitat fragmentation and fewer land-use changes (Pearson and Dawson, 2003), coupled with the shorter lifespan of many marine species, the predominance in many benthic species of sessile adults that are unable to move away from unsuitable conditions (Newell, 1979) and pelagic larval stages with high dispersal potential (Burrows et al., 2011; Gaines and Bertness, 1992; Roughgarden and Feldman, 1975).

A generalized prediction is that biogeographic ranges of species will shift polewards in response to the polewards movement of seasonal isotherms as the global climate warms (Lodge, 1993; Lubchenco et al., 1993). Suitable habitat exists beyond the distributional limits of many species of plants (Grace, 1987; Woodward, 1987), mammals (Andrewartha and Birch, 1954; Graham and Grimm, 1990), birds (Root, 1988) and marine invertebrates

(Kendall and Lewis, 1986; Lewis, 1964) but the unsuitability of environmental conditions currently prevents their colonization and therefore the ranges are assumed to be limited by climate. Alternatively, the range edge may lie some distance inside the 'envelope' of suitable climate space due to local factors such as a lack of suitable habitat, poor dispersal and connectivity of suitable habitat space (Kendall, 1987) or if biological interactions are important in setting distributional limits.

Global 'fingerprints' of climate change do indeed show coherent patterns of range shifts (Root et al., 2003) at an average rate for 857 species of 72.0 ± 13.5 km per decade of the leading range edge and 15.4 ± 8.7 km of the trailing range edge towards the poles (Poloczanska et al., 2013), illustrating that the impacts of global warming are already apparent. The rate of change to intertidal species and systems is greater than for terrestrial systems (Cheung et al., 2009; Mieszkowska et al., 2014a,b; Poloczanska et al., 2013), however, the response to a global rise in temperature can be spatiotemporally variable and species specific, highlighting the problems associated with generalizations for predicting the pattern of movement within a given species range limit.

8.2 Changes in Population Dynamics

Temporal changes in species abundances within populations have also been recorded for coastal birds (Lusk et al., 2001; Thompson and Ollason, 2001; Veit, 1997; Veit et al., 1996), mammals (Stenseth et al., 1999), zooplankton (Roemmich and MacGowan, 1995), intertidal invertebrates (Barry et al., 1995; Murray et al., 2001; Sagarin et al., 1999; Southward et al., 1995), fish (Beaugrand et al., 2003; Genner et al., 2004; McFarlane et al., 2000) and corals (Sheppard, 2003). Increasing numbers of species from warm climatic regions are expected to replace those with colder climate affinities, leading to alterations in the composition of local assemblages (Barry et al., 1995; Holbrook et al., 1997; McGowan et al., 1996; Sagarin et al., 1999; Southward et al., 1995). These local scale changes will also facilitate the poleward spread of species by altering the ratio of extinction to colonization events within range edge populations (Parmesan et al., 1999). There is a general pattern evident across a wide range of marine and terrestrial taxa of the highest population densities occurring at the centre of distribution of a species, with abundances decreasing towards the range edges (Brown, 1984). A positive relationship between abundance and geographic distribution has been identified for many coastal marine species; however, the spatial

and temporal coverage of past data have often made it difficult to resolve whether increases or decreases in species abundance represent actual changes in biogeography, or merely fluctuating population dynamics within a species range, raising questions as to the general validity of this hypothesis for marine benthic systems (Barry et al., 1995; Murray et al., 2001; Parmesan et al., 2005; Veit, 1997). There are also several exceptions to this pattern in marine species, including kelps, with populations located in the centre of the biogeographic distribution being as vulnerable to climate change as populations at the range edges (Bennett et al., 2015; Wernberg et al., 2016).

The goals of current research into biological processes by which species respond to climate change are to unravel the mechanisms by which each species is responding to multiple stressors, and to apply this knowledge to modelling past, current and future responses of benthic species to climate change and ocean acidification within the marine environment.

8.3 Biological Mechanisms

The possibility of differential rates and extents of climate warming between local and regional scales may also result in variations in the biological responses (Schneider and Thompson, 1981; Washington and Meehl, 1989). In order to accurately predict the rate and extent of future biogeographic shifts in species distributions, the biological mechanisms driving these changes need to be better understood. Physical, ecological, evolutionary and physiological factors acting on the processes of reproduction, birth, dispersal, recruitment and mortality are all involved in shaping species' ranges (Brown et al., 1996; Carter and Prince, 1981; Lennon et al., 1997; Lodge, 1993) and must also be considered when studying the effects of a changing environment. These processes operate predominantly at the local scale, and the effects of environmental change will be most apparent at the population and metapopulation level (McCarty, 2001). Close to the poleward distributional limits of a species, populations will be exposed to environmental temperatures (i.e. cold) which approach their thermal tolerance limits more often than at locations in the centre of the range (Bertness et al., 1999; Fields et al., 1993; Wethey, 1984). Physiological tolerances of individuals to adverse conditions will determine individual survival and maintenance of the local population, and may shape the range limits as a direct result (Bauer, 1992; Lewis, 1986; Lewis et al., 1982; Newell, 1979). In addition, range limits may also be affected by the timing of low tides within intertidal environments, as low water springs occurring during

the centre of the day will expose species to higher temperatures, whereas night-time low water spring tides will result in exposure to cold stress at the high latitude, leading range edges for intertidal species (Helmuth et al., 2002; Mieszkowska et al., 2007).

The role of climate signals in the timing of phenological events in terrestrial plant and animal species is already well understood (Walther et al., 2002). Similar changes are being documented in marine systems, with peak abundance of phytoplankton and zooplankton in the North Sea (Edwards and Richardson, 2004), prespawning migration events in squid (Sims et al., 2001), spawning in fish (Sims et al., 2004) and intertidal limpets (Moore et al., 2011) occurring earlier each year in the 2000s than in the 1980s. Nearly all phenophases show strong correlations with spring temperature with a 1-month time lag, indicating that these shifts are being driven by climate warming (Walther et al., 2002). The variation in the timing of reproductive events suggests that many responses may be species specific, and may lead to changes in timing of life stages in relation to the availability of food sources and alterations in competitive, predatory and mutualistic interactions between species (Bertness et al., 1999; Davies et al., 1998).

Critical temperatures are directly connected with the process of reproduction at the larval stages and in those species that metamorphose to sessile benthic stages (Hutchins, 1947; Orton, 1920; Thorson, 1946). Adaptations to heat tolerance have been evidenced across geographic locations or associated with the transitions from one habitat to another, through the role of biological mechanisms and behavioural thermoregulation ameliorating the impacts of extreme temperatures. Despite this, the vulnerability to continued warming will always differ across species, habitats and localities (Marshall et al., 2013) where some species will suffer negatively (Bartsch et al., 2013).

Cold water species are thought to be more resilient than warm water species and are better able to cope with longer periods of adverse conditions (Helmuth et al., 2006; Mieszkowska et al., 2006a; Southward, 1967; Southward et al., 1995). In these situations, they may grow slower, ceasing their reproductive growth and offspring production, but may still persist in an ecosystem with their reproductive output sufficient to maintain local populations if conditions become amenable for them to do so. This phenomenon was described by Southward (1967) and Southward et al. (1975, 1995), who observed southward range expansions of cold water intertidal barnacles associated with cooling SST pulses, followed by warmer periods during which these populations were able to maintain their extended ranges. It is known that warm water species generally grow faster

and reproduce earlier during their shorter life extent compared with cold water congeners (Lewis, 1986). Thus, it is reasonable to expect that geographical responses to climate warming will be noticed earlier for warm water species, because their life cycle characteristics confer them a more opportunistic character. Also, in a warming scenario, the new environmental conditions will allow southern species to expand their range northwards, thus releasing them from competitor and predator pressures, although potentially exposing them to new competitive or predatory species interactions. Conversely, native cold water species still have to interact with coevolved competitors, predators and diseases in addition to the invaders, which might decrease their fitness (Sax and Brown, 2000).

It has been shown that the distributions of both terrestrial (e.g. Brooker, 2006) and marine organisms (e.g. Connell, 1961; Wethey, 2002) are conditioned not only by the physical environment but also by biological interactions, and that the responses to the environment can themselves be affected by biotic factors like competition and predation (Richardson and Schoeman, 2004; Sanford, 2002). An increase in competition between cold- and warm water species is expected if warm water species are shifting polewards while cold water species are not moving or only moving by chance both southwards and northwards (Lima et al., 2007a).

9. FUTURE ADVANCES IN QUANTIFYING AND MODELLING DISTRIBUTIONAL RESPONSES TO CLIMATE CHANGE

9.1 Standardizing the Recording and Availability of Data on Species

There are still few coordinated, standardized monitoring programmes for intertidal and subtidal rocky and soft sediment habitats and ecosystems that span multiple countries across the seas of the Northeast Atlantic region, resulting in limited monitoring and data for species distributions at local, regional or national scales (Mieszkowska et al., 2006b, 2014b; Raybaud et al., 2013). Data and knowledge on the current distribution, temporal trends and important drivers, is fragmented and often outdated, with differing methodologies across countries, habitats and faunal groups, creating difficulties when attempting temporal assessments of biodiversity at the national and continental scales (Hummel et al., 2015; Steneck et al., 2002; Wells et al., 2007).

Several multinational organizations have established networks, online information resources and databases to combine the available data and promote collective work at the international level to address the problem of conserving biodiversity in the face of global challenges such as climate change. At the global scale, the International Union for Conservation of Nature (IUCN), the world's oldest and largest global environmental organization, is a neutral forum for governments, NGOs, scientists, business and local communities to find practical solutions to conservation and development challenges. At the regional level, organizations include the OSPAR Commission, comprised of member states on the western coasts and catchments of Europe, together with the European Union (OSPAR, 2016). OSPAR has been allocated the role of the competent regional organization guiding international cooperation on the protection of the marine environment of the North-East Atlantic. The role of OSPAR is to 'harmonize policies and strategies, including the drawing up of programmes and measures, for the protection of the marine environment' and to undertakes and publishes at regular intervals joint assessments of the quality status of the marine environment and of the effectiveness of the measures taken and planned. The OSPAR North-East Atlantic Environment Strategy is taking forward work related to the implementation of the Ecosystem Approach to partially address the data issues at the species-specific level. In addition, there are now organizations and resources such as the extant data repository EurOBIS (EurOBIS, 2016), that are providing a central point to search for data and the UK-run MEDIN data partnership for marine observing systems (MEDIN, 2016) and previous datasets such as the Marbef funded LargeNet project (LargeNet, 2016).

Assessments from these data repositories and wider searches of the academic and governmental publications and databases show that large-scale spatial trends for many marine species in Europe are difficult to identify as a result of one or more reasons: (i) the lack of available long-term quantitative datasets in large parts of the geographical distributions across part, or all of Europe; and (ii) the occurrence of small-scale spatial variability due to either natural or anthropogenic forcing factors, with some species increasing in parts of their geographical distribution but decreasing in other areas, in some cases occurring only a few kilometres apart from each other. Additionally, contrasting trends for the same species have documented at different depths or due to local small-scale variations, e.g. wave exposure, even within the same habitat or coastline area.

9.2 Developing Scientific Methodologies for Quantifying Previous, and Modelling Future Changes in Species Distributions in Response to Climate Change

Understanding and predicting current and future responses to global climate change is one of the greatest challenges facing science today. This chapter has already dealt with the developments and issues facing the collection of broadscale and long-term field data on species distributions, and touched on the need for new, biologically mechanistic information that is also required to accurately attribute cause and effect within the complex problem of determining species responses to global climate change.

Forecasts of future biological responses to climate change are often required to incorporate the interaction of multiple climatic and nonclimatic stressors at far smaller spatiotemporal scales than provided by international climate models and scenarios, in order to be of use to today's scientists, policymakers and managers. The desire for generalizations in climatic change and biological responses has meant that often, scientific predictions of ecological responses to climate change, and the design of experiments to understand underlying mechanisms, are too often based on broadscale trends and averages that at a proximate level may have little relevance to the vulnerability of organisms and their ecosystems (Helmuth et al., 2015b).

Most existing models of climate change, field-based recording or monitoring studies and many laboratory experimental systems, are, however, too coarse in resolution, and too simplistic to incorporate data at the microclimate scale. Such small spatiotemporal resolution information on climatic data, however, is required to provide realistic environmental changes at the scale at which marine organisms are reacting to changes in the thermal environment, and which will ultimately drive geographic-scale changes in species distribution patterns (chapter "Cross-scale approaches to forecasting biogeographic responses to climate change" by Torassian et al. in this volume). In environments where temperature is a limiting factor for biological processes and organismal survival and reproduction, small differences in microtopography within the habitat mosaic can create strong microclimatic differentials over short distances and allow persistent microclimatic refuges to develop (Coulson et al., 1995).

There is thus an urgent need for the research community to create biologically relevant metrics and models of climate change and climate change impacts, incorporating both the processes by which large-scale climate change trains the smaller scale, but organism relevant weather systems, and information on how organisms, and ultimately ecosystems respond to

these climatically driven changes (Helmuth et al., 2015b). Such an approach is likely to offer relevant information on those physical aspects of climate change will be most relevant to monitor and predict, and also increase the ability to communicate the impacts of climate change to governmental, conservation and public sectors engaged in the development and acceptance of climate change policies (Spencer et al., 2012; chapter "Cross-scale approaches to forecasting biogeographic responses to climate change" by Torassian et al. in this volume).

The coastline and shallow marine ecosystems around the British coastline are some of the most extensively studied systems globally, providing some of the longest biological time-series globally on changes in distribution and abundance for the coastal marine species (Mieszkowska et al., 2005, 2014b; Southward et al., 2004a). Less spatiotemporally extensive or continuous survey data exist for specific taxa or habitats along the wider spatial extent of the European coastline, as described in Section 7. The central, online repository of these datasets is advancing the understanding of species distributions, ecosystem structuring and impacts of climate change from the small scale, individual site-based level up to the larger, continental scale.

In addition to these developments in survey and time-series data availability are the development of both climatic data and models at spatiotemporal scales relevant to individual organisms and changes in the thermal habitat over small areas of metres to kilometres (e.g. microclimatic data) (Helmuth et al., 2006; Kearney et al., 2012), and physiological models capable of translating the organismal response to changes in climate up to the biogeographic scale relevant to entire species. These biophysical-ecologically coupled dynamic energy budget models are now being developed for marine species in the Northeast Atlantic region, and appear promising in their predictions of current and future distributions of both commercial and ecologically important marine species (Kearney et al., 2010, 2012; Sarà et al., 2011, 2014). This trait-based bioenergetic mechanistic approach for predictions of life history traits in marine organisms show great promise for addressing the problems currently faced by scientists, conservationists, reserve managers and policymakers when attempting to determine the spatiotemporal effects of global climate change, and consolidates the various scientific disciplines required to record, test and forecast climate-driven changes to marine species.

Long-term observations enable the prediction and exploration of future scenarios via experimental testing in the field and laboratory as well as the creation of correlative predictive models of future locations of biogeographic distributions for species. Sustained observations are essential to

disentangle natural long-term variability from anthropogenic drivers of change. In addition, targeted physiological studies to determine and quantify biological mechanisms underpinning the responses of marine benthic species to climate change and ocean acidification will provide a new understanding of how individual organisms respond to changes in their thermal environment, and quantify performance across a gradient of sea and air temperatures within coastal ecosystems. These mechanistic data can be input into biomechanistic models, capable of producing biologically relevant measures of organismal performance when exposed to specific thermal regimes at any geographic location across the biogeographic range of a species. This integrated research concept provides new and innovative multidisciplinary approach to comprehensively track and understand species responses to current and future global climate change.

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